Implications of biological and physical diversity for resilience and resistance patterns within Highly Dynamic River Systems

Eric Tabacchi[1,*], Johannes Steiger[2], Dov Corenblit[2,3], Michael T. Monaghan[4] and Anne-Marie Planty-Tabacchi[1]

[1] Université de Toulouse III, ECOLAB - Laboratoire d'écologie fonctionnelle, UMR 5245 CNRS/UPS/INPT, 29 rue Jeanne Marvig, 31055 Toulouse Cedex 04, France
[2] Clermont Université, GEOLAB - Laboratoire de géographie physique et environnementale, UMR 6042 CNRS/Université Blaise Pascal, Maison des Sciences de l'Homme, 4 rue Ledru, 63057 Clermont-Ferrand Cedex 1, France
[3] King's College London, Department of Geography, Strand London WC2R 2LS, U.K.
[4] Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Mueggelseedamm 301, 12587 Berlin, Germany

Abstract. The structure and function of alluvial Highly Dynamic River Systems (HDRS) are driven by highly variable hydrological disturbance regimes, and alternate between resistant, metastable states and resilient, transitional states. These are in turn subject to influences of feedback loops within hydrogeomorphic and biological processes. Here we consider how resistance and resilience largely determine HDRS ecosystem trajectories and how these characteristics can be modified by natural and anthropogenic processes. We review the mechanisms by which biodiversity can affect both resistance and resilience and introduce a conceptual framework that incorporates some unique HDRS characteristics. We suggest that resilient and resistant patterns frequently coexist in the active tract of these river systems, and that this coexistance promotes the return of metastable states after major disturbances. In contrast, highly resistant and poorly resilient patterns dominate at their external boundaries. The loss of these natural dynamics resulting from direct and indirect human impacts causes deviations to resistance and resilience patterns and therefore to HDRS trajectory. We propose that understanding the role of interactions between biological and physical processes that control resistance and resilience is crucial for system restoration and management.

Key words. Resilience; resistance; biodiversity; river system; fluvial geomorphology; ecological community.

Introduction

Highly dynamic river systems (HDRS) in alpine areas typically contain braided and island-braided channels (cf. Beechie et al., 2006 for a definition) and concentrate steep energy gradients within wide river corridors that undergo frequent change (10^0 – 10^1yrs) (Frissell et al., 1986). More than in other types of rivers, HDRSs contain a mosaic of patches within the river corridor that are at different states along an ecological trajectory. Patches may be metastable, i.e. in equilibrium but susceptible to change to a lower-energy state when exposed to only small perturba-

* Corresponding author e-mail: eric.tabacchi@cict.fr

tions, or patches may be unstable. For example, Van der Nat et al. (2003) showed that approximately 60% of the aquatic habitats and 30% of the vegetated islands in the active tract of the Tagliamento River (Italy) were renewed every 2.5 years. Along an upstream-to-downstream gradient of the same river, Arscott et al. (2002) similarly demonstrated that the habitat turnover rate was approximately 62% in braided headwater reaches, compared to only 20% in low energy, meandering reaches. The diversity of patches results from complex feedback mechanisms between physical and biological processes that vary in space and time in response to hydrogeomorphic disturbance events (Tal et al., 2004; Gurnell and Petts, 2006). These feedbacks, along with the functional and physical connections between the river corridor and its surroundings, result in self-organizing system processes (e.g. ecological succession, species migration, energy dissipation, channel adjustment). These processes can be observed in most river ecosystems (Kalliola and Puhakka, 1988; Malanson, 1993; Naiman and Décamps, 1997; Poff et al., 1997; Tabacchi et al., 1998; Tockner et al., 2000; Van der Nat et al., 2003; Naiman et al., 2005); however, while the relative importance of these processes generally follows a continuous gradient, we argue that in HDRSs they occur in discrete steps.

Despite their importance, our understanding of the physical and ecological controls of HDRS dynamics remains fragmented in the literature, and few studies have attempted to integrate both physical and biological controls into a conceptual framework. The core objective of the present paper is to contribute to such a framework by reviewing the literature on riverine ecosystems that are prone to high levels of natural disturbance, and by highlighting the role of three emergent properties: resilience, resistance, and diversity. These properties have both physical and biological components, and an important part of our review is to investigate how each of these may differentially contribute to HDRS dynamics. We place a special emphasis on the distribution of resilience, resistance, and diversity across transverse environmental gradients from the active tract of the fluvial corridor to the riparian floodplain. This perspective is facilitated by a number of landscape- and ecosystem-level studies (e.g., Ward et al., 2002; Tockner et al., 2003; 2006; Allan, 2004) that, because of the scale considered, are more likely to highlight these properties.

HDRS core emergent properties and related processes

Disturbance

Disturbance can be generally defined as any force that tends to move the system's trajectory far from a given equilibrium (steady state). By analogy to physical systems, early studies of the functional trajectories of ecosystems (e.g., May, 1997) included resistance and resilience to disturbance as core emergent properties; that is, complex properties that arise from a number of relatively simple interactions. Most ecosystems are prone to physical disturbance, but riverine systems are often considered as explicitly disturbance-driven (Resh et al. 1988; Malanson, 1993; Naiman et al., 2005; Lepori and Hjerdt 2006). Physically, riverine disturbance includes large hydrological events that promote the erosion, transport, and deposition of large amounts of sediment. Droughts can also be considered as a physical disturbance in river systems, since they can lower substrate cohesiveness (Corenblit et al., 2007). Biological invasions are also considered as disturbances to river systems, but will be discussed in the context of resistance (i.e., organisms' response) below.

The classification of disturbance events is context-dependent, but disturbances with intermediate frequency, intensity, or duration are thought to generate greatest physical diversity (Connell, 1978). Ecological disturbance typically results from similar hydrologic forces, but can be defined as an unpredictable event that delivers physical injury to living organisms. This is in contrast to stress which is predictable and tends to constrain physiological performances (Grime, 2001). In practice, ecological disturbance can be extended to population, community, and ecosystem scales as a disruption of the physical habitat structure. According to the timing, frequency, magnitude, intensity, and spatial extent of the perturbing event, only some populations or patches may be altered at a given scale, and therefore recognize a given event as a disturbance.

Disturbance is recognized as a driving force of ecological succession, largely as a determinant of ecological strategies of the organisms responding to the magnitude and timing of disturbance along a successional gradient. Holling (1986) and Carpenter et al. (2001) described the adaptive cycle of a natural metastable system as a succession of characteristic phases after a major disturbance event: rapid growth and exploitation (r); conservation (K); release or 'creative destruction' (Ω); and renewal or reorganization (α). The ecological role of intermediate levels of disturbance in promoting high levels of biodiversity has been widely discussed since the early work of

Connell (1978). In riverine ecosystems, such biodiversity gradients have been described as correlated to the habitat diversity (Naiman and Decamps, 1997; Townsend et al., 1997; Pollock et al., 1998; Tabacchi et al., 1998; Ward et al., 2001; Mouw and Alabak, 2003), although finer biological interactions have also been invoked to explain this pattern (Miller and Chesson, 2009). These biodiversity peaks are expected to occur within the piedmont zone and in the middle course along HDRSs (Tabacchi and Planty-Tabacchi, 2001; Arscott et al., 2002; Mouw and Alabak, 2003), but also across the margins of the active channels in the transverse dimension (Pollock et al., 1998). Intermediately disturbed, meandering river systems exhibit very high to exceptional levels of regional and local biodiversity (e.g. Planty-Tabacchi et al., 1996; Pollock et al., 1998), whereas HDRSs commonly address lower levels of biodiversity and truncated successional series because of the greater frequency of large hydrogeomorphic disturbance events (Gurnell et al., 2001; Corenblit, 2006).

Resistance

Resistance can be defined as the ability of the system components to maintain similar trajectories in the face of potential disturbance events. Physically, natural systems cannot remain permanently resistant. They can therefore be considered as metastable systems, with successive steady states separated by thresholds. Several ecological attractor states (recurrent states that remain invariable under low levels of disturbance) have been recognized in the trajectory of natural systems (Holling, 1973, 1986; Gunderson and Holling, 2002). Another concept of ecological resistance, namely the resistance to ecological succession, initially was developed in the perspective of biological invasions (Elton, 1958; D'Antonio and Thomsen, 2003). Ecological resistance can be further extended in HDRSs by including ecological strategies of living organisms to face physical disturbance (Mitchell et al., 2000; Odling-Smee et al., 2003).

Whereas meandering river systems appear poorly resistant to hydrological disturbance because of their continuous gradients of morphological changes, HDRSs are characterized by 'stepwise', patchy changes, suggesting periods of high resistance to disturbance. Inheritance mechanisms (e.g., successive droughts, successive accretion events) may control local physical resistance, so that two similar disturbance events do not have necessarily similar consequences for a given site (Werritty, 1997). Vegetation plays a major role in controlling the landscape dynamics of HDRSs, although it is difficult to quantify its effect in terms of landscape parameters in the field (Tabacchi et al., 1998; Gurnell et al., 2001). Flume simulations (Tal et al., 2004; Coulthard, 2005) suggest that the density of colonizing riparian vegetation that is resistant to the natural hydrogeomorphic disturbance regime controls the braiding index of HDRSs.

The permeability of the HDRS corridor boundary to matter and energy flows (i.e., its physical resistance) also can be considered as a measure of ecological resistance. At the landscape scale, river system boundaries play a major role in the regulation of energy and matter flux (Newbold et al., 1981, Naiman and al., 2005; Steiger et al., 2005). At a more local scale, among-habitat permeability can be observed within the riparian ecosystem, as shown for terrestrial invertebrates (Stanford and Ward, 1992; Tabacchi, 1992; Deharveng and Lek, 1995; Collier et al., 2002; Paetzold et al., 2005).

Ecological permeability along rivers has typically been treated in the context of biological invasions by alien species (Tabacchi and Planty-Tabacchi, 2001; D'Antonio and Thomsen, 2004) or non-riverine native species (Tabacchi and Planty-Tabacchi, 2001). Elton (1958) predicted that species-rich communities would be more resistant to invasion, with competition acting as a barrier. Although this hypothesis remains controversial (D'Antonio and Thomsen, 2004; Tabacchi and Planty-Tabacchi, 2005) HDRSs are likely to be highly vulnerable to biological invasions because they combine moderate levels of biodiversity and high-frequency disturbance. These properties are linked, because the effect of boundary permeability on community diversity seems to depend on the disturbance regime (Tabacchi and Planty-Tabacchi, 2001). Disturbance can modulate the severity of the invasion by altering the response of local communities. Natural hydrologic disturbances do not prevent the introduction of such species, mainly due to the physical permeability of the corridor, but probably prevent a sudden drop in pioneer plant community diversity by enhancing resource availability (including unoccupied space) and species turnover, and relaxing interspecific competition (Davis et al., 2000). Intact braided rivers also seem to be prone to biological invasions due to their natural dynamics (Mouw and Alabak, 2003; Williams and Wiser, 2004) that promote longitudinal dispersion of invasive species propagules and a wide diversity of available habitats when introduced species are present in the immediate surroundings. Similarly, Crowl et al. (1992) observed the introduction of the alien brown trout in Australian rivers to result in fragmentation of the native galaxiid fish populations which could not resist invasion at the nodes of the hydrological network.

Resilience

Resilience can be defined as the ability of a system to tolerate or absorb perturbations or disturbance without changing to a qualitatively different state that is controlled by a different set of processes. Since the introduction of the concept of ecosystem resilience by Elton (1958), several definitions remain widely used (Grubb and Hopkins, 1986; Lavorel, 1999). Brierley and Fryirs (2005, p. 205) argued that resilient rivers are able to adjust to perturbations and that the physical ability of a system to absorb these perturbations, such that disturbance events do not elicit a morphological response, is referred to as the buffering capacity.

Resilience can be quantified as a measure of how fast a system returns to its equilibrium state after a disturbance (i.e., 'engineering resilience', Holling, 1996). Implicit in this definition is that the system exists near a single equilibrium condition, and that we can measure how far the system has moved from equilibrium and how quickly it returns. The amount of disturbance that an ecosystem could withstand without changing self-organized processes and structures was also defined through alternative stable states ('ecological resilience' *sensu* Holling, 1973). One key distinction between engineering and ecological resilience lies in assumptions regarding the existence of multiple stable states, and several authors have made subtle amendments to this definition (Peterson et al., 1998; Carpenter et al., 2001; Gunderson and Holling, 2002; Walker et al., 2004).

Aside from individual strategies or behaviors of organisms, biodiversity also may form one of the major components of ecological resilience. At the local scale, biodiversity can be primarily viewed as a reflection of the diversity of available resources, weighted by the ability of the organisms to share or optimize the uptake of these resources at the community level (cf. Chase and Liebold, 2003). At the community level, Grubb and Hopkins (1986) proposed that resilience of organisms' abundance would be a positive function of the species richness of the community, up to the point that all possible regeneration strategies are fully represented. Perhaps, the most obvious 'role' of biodiversity in ecological systems is the 'insurance' for ecosystem functioning that is promoted by high numbers of populations (species) facing a disturbance event (Walker, 1995; Chapin et al., 1997; Yashi and Loreau, 1999; Hooper et al., 2005). However, high species numbers only do not ensure *per se* a high resilience of the system. Resource availability also regulates biotic interactions within ecological communities (Huston, 1994).

Coexistence of HDRS resistance and resilience

Resilience and resistance can co-occur in HDRSs. Post-disturbance dynamics involve self-adjustment processes between biological and physical compartments, restoring metastable conditions of system functioning close to the variability observed in the basic trajectory of the system prior to disturbance. However, such self-adjustments may fail if resistance- or resilience-related mechanisms cannot fully operate (Roxburgh et al., 2004). In this case, the system may establish a trajectory toward an alternative steady state, different from the one prior to the disturbance event. Conversely, a prolonged absence of disturbance events may direct the system trajectory toward mature stages of ecological succession and generate a system more resistant to events with certain levels of flood magnitude (Naiman and Decamps, 1997; Gurnell and Petts, 2006). We can therefore hypothesize that the stochastic, patchy pattern of HDRS landscapes results from an episodically revised trade-off between local resistance and local resilience. The existence of this trade-off would suggest that the two properties can locally co-occur within the HDRSs environmental gradients.

The internally dynamic character of HDRS corridors (*sensu* Forman and Godron, 1986) results in an irregular gradient of stability from the active tract to the external edge of the natural riparian vegetation. Hence, a strong functional disruption (or sharp gradient) is expected between the active tract and alluvial bars and the floodplains where biological interactions become increasingly dominant (Corenblit et al., 2007). In this context, thresholds in system dynamic changes (Folke et al., 2004) are not only controlled by the magnitude of isolated disturbing events (i.e., extrinsic thresholds), but also by local resistance, which depends upon historical sediment depositional dynamics (e.g., the formation of accretion bars, large woody debris deposition) and ecological succession (e.g., maturity of the vegetation). As a result, the long-term dynamics of such systems include contraction and expansion periods, during which the ratio between the active tract area and the floodplain area can change significantly (Ward and Uehlinger, 2003). From a successional point of view, the Carpenter et al. (2001) model described above is truncated in HDRS to r, Ω and α phases within the active tract, with the K phase existing only at the outer boundaries of the active tract (e.g., mature, non-pioneer forests) or within deep groundwater compartments (Edwards et al., 1999; Gurnell et al., 2001; Corenblit et al., 2007).

These characteristics allow us to clarify the overall positioning of HDRSs in comparison to other fluvial

styles according to their responses to disturbance, in terms of resilience and resistance. Whereas channelized rivers typically exhibit high levels of overall physical (but not biological) resistance and low levels of physical and biological resilience, meandering systems show high levels of resilience and moderate levels of resistance (Fig. 1). The arguments presented above allow us to hypothesize that moderate levels of resistance can coexist with high-to-medium levels of resilience in HDRSs.

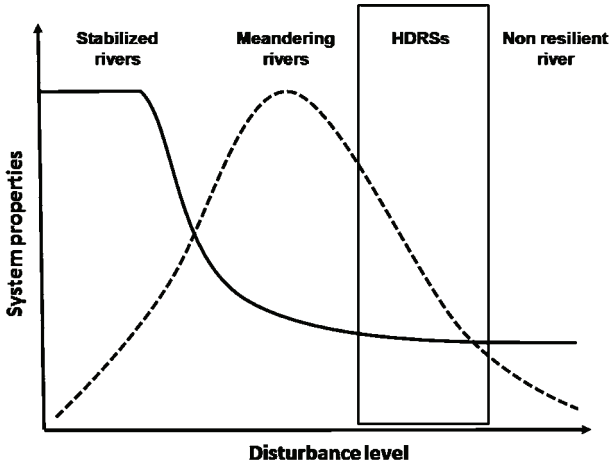

Figure 1. Theoretical positioning of HDRSs among other types of river systems along a natural gradient of flood disturbance. Lines represent two hypothesized levels of system properties: overall resistance (solid line) and resilience (dotted line) within the river corridor.

It is important to consider resistance and resilience together in the context of biological interactions and ecological strategies. Resilience patterns are mainly supported by r-strategists, which provide labile and easily dispersed populations. Although this pattern appears obvious for plants (annual and biennial species), some animals are easily dispersed by flows (passive drift) at the imago or egg stage. Egg resistance to desiccation is well documented for several micro- and macro-crustaceans, some of them (*Notostraca* and *Conchostraca*) being particularly well adapted to temporarily inundated areas (Eder et al., 1997). Most riparian arthropods can survive temporary flood events by actively or passively finding refugia in the sediment (e.g., Lude et al., 1999).

Across the transverse gradient of the fluvial corridor, resistance and resilience may be quite differently distributed. Within each of the two major areas of the HDRS corridor (Fig. 2), we typically observe a characteristic, patchy mosaic of habitats. This mosaic is not limited to the surface, since hyporheic or phreatic (subterranean) compartments are also known to be highly patchy (Malard et al., 2002). The main channel is directly exposed to the higher energy flows, and therefore will exhibit low physical and biological resistance, whereas resilient processes are expected to be more important. The maximum resilience level is expected within the active tract, adjacent to the main channel, where labile islands develop. Together with high resilience, high resistance occurs due to the development of fast-growing woody vegetation. This area, where the shoreline dynamics attain their maximum frequency, constitutes one of the major internal HDRS ecological gradients (Corenblit et al., 2007). The further transition between this area and the active alluvial terraces corresponds to a positive gradient of resistance and a negative gradient of resilience, as physical drivers are progressively replaced by biological drivers. At the higher elevations of the active river corridor, the potential resilience processes remains (for example, through a buried persistent seed bank), and the development of old stands of riparian forest provides a high degree of physical resistance. In most HDRSs, sharp transitional gradients, often acting as ecological barriers, are observed between alluvial and non-alluvial vegetation, largely due to important topographic slope (uplands) or to human influence (lowlands).

HDRS characteristics largely result from the timing of large, low frequency, disturbance events. Even though the hydrological regime of these river systems is often driven by annual snowmelt, followed by a drought period, interannual variation in precipitation broadly controls the landscape stability. Classically, this macro-stability tends to increase from the active tract where the energy flows concentrate during floods, eroding and depositing coarse sediment, to the external boundary of the river corridor, where surface hydrological processes tend to be disconnected due to higher surface elevations. However, the interaction between purely physical and biological processes tends to locally modify this overall gradient. From a successional perspective, pioneer plant communities are expected to exhibit higher levels of resilience related to recolonization ability, whereas later successional stages are expected to show higher levels of resistance, due to the selection of more competitive species by stable environments.

The capacity of organisms to regenerate and therefore promote resilience (Bellingham and Sparrow, 2000; Barsoum, 2002; Klimesova and Klimes, 2007) is most commonly considered in reference to the plant communities that are involved in mid- to late successional stages, but pioneer species (e.g., willows and poplars) can alternate clonal and sexual reproduction in braided systems (Gom and Rood, 1999; Barsoum, 2002). A significant regeneration from resistant vegetated islands can be observed in

HDRSs (Kollmann et al., 1999). A contrasting strategy can be developed at the population level by dispersal modes that match the current disturbance regime (Tabacchi, 1995; Mahoney and Rood, 1998; Andersson et al., 2000; Middleton, 2000; Tabacchi et al., 2005). Such dispersal strategies are developed in pioneer plant communities (ruderal strategy, *sensu* Grime, 2001; Southwood, 1988) or in early invertebrate succession (Tabacchi, 1992; Tockner et al., 1999; Ward and Tockner, 2001; Amoros and Bornette, 2002; Latterell et al., 2006). In HDRSs, animals may migrate to escape temporary disturbance (Ballinger et al., 2007) or may colonize newly created aquatic habitats (Robinson et al., 2002; Malard et al., 2006). The diversity of patterns developed in HDRSs would explain the expectancy of co-occurrence of multiple pathways of resilience, depending on the successional stage of given patches within the changing habitat mosaic (Cooper et al., 2003).

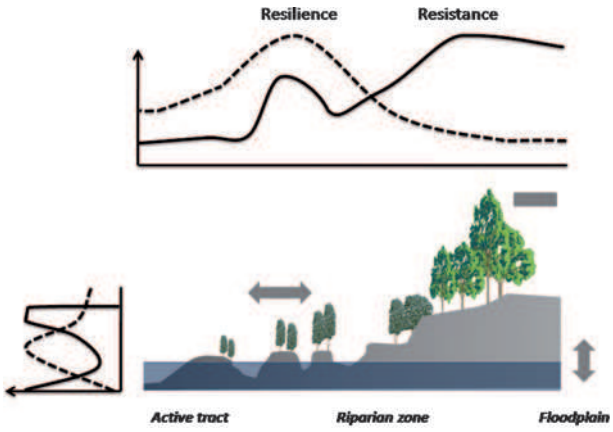

Figure 2. Theoretical horizontal and vertical distributions of resistance (solid line) and resilience (dotted line) across the riparian corridor profile of a Highly Dynamic River System. Grey arrows and blocks indicate major permeability hotspots and barriers, respectively. See text for explanations.

Physiognomic diversity of the vegetation (i.e., the spatial organization and the internal physiognomy of patches) has been shown to be a crucial control of resilience and resistance in HDRSs (Corenblit et al., 2007). The combination of sedimentary accretion points and resistant vegetation structures may then initiate an overall stability of the corridor through ecological feed-backs between the active tract and the less disturbed areas, which can be locally increased by efficient root systems (Kollmann et al., 1999; Gyssels et al., 2005; Gurnell and Petts, 2006). Studies of riparian vegetation have observed shrubby pioneer plant communities to deliver resistant (flexible) structures in or near the active tract, where perennial or annual herbaceous mats can also efficiently protect the substrate from erosion. These species correspond to "ecological engineers" (*sensu* Jones et al., 1994, reviewed by Corenblit et al., 2008). In Europe, species like *Agrostis stolonifera* (native) or *Paspalum paspaloides* (introduced) play such a role (Tabacchi, 1995; Corenblit, et al., 2007). Pioneer shrubby *Salicacea* such as *Salix eleagnos* or *S. purpurea*, or *Tamaricacea* such as *Myricaria germanica* in HDRSs are flexible enough to resist to moderate flows, protecting a narrow strip along the channels of the active tract, and frequently resprouting when buried (Karrenberg et al., 2002; Corenblit et al., 2007). During severe floods, these and other plant species (e.g., *Populus nigra*, *P. alba*, *Salix alba, S. fragilis*) can be entirely buried in the sediment and resprout after disturbance (Barsoum, 2001; Gurnell et al., 2001; Gurnell and Petts, 2006; Corenblit et al., 2007).

From HDRS vulnerability to HDRS restoration

Closely related to resistance is the concept of sensitivity, or the propensity of a system to respond to a minor external change (Schumm, 1991, p.78). Brunsden (2001, p.99) defined landscape sensitivity as "the likelihood that a given change in the controls of a system or the forces applied to the system will produce a sensible, recognizable, and persistent response". Sensitivity is thus a function of the spatial and temporal distributions of the resisting and disturbing forces. Inherently dynamic ecosystems, such as HDRSs, appear to be highly sensitive not only to natural disturbance, but also to disturbance induced by human activities. HDRSs are increasingly altered by human activities throughout the World (Muhar et al., 1998; Andersson et al., 2000; Bunn and Arthington 2002; Tockner et al., 2003; Sadler et al., 2004; Poff et al., 2007) and their functional and structural integrity is increasingly endangered by direct human impacts (river training works, dam and levee construction, gravel mining, bank protection; e.g., Nilsson and Berggren, 2000) as well as global climatic and environmental change (Macklin and Lewin, 2008). Management practices directly act on the physical structure of the fluvial landscape, inducing habitat homogenization and landscape fragmentation (England and Rosemond, 2004).

Responses to changes in landscape patterns and dynamics following either artificial shifts in disturbance regime or physical fragmentation of habitat (e.g. Allan, 2004; Tetzlaff et al., 2007) are also frequently illustrated by biological invasions in the aquatic ecosystem itself (Jones et al., 2000) or in the riparian ecosystem (Stachowicz et al., 1999; Tabacchi and Planty-Tabacchi, 2001; Johnson et al., 2008). Several

examples have also shown the extent to which flow regulation can induce massive colonization and population growth by native plants, increasing the lateral stability of the riparian corridor and limiting the original successional pathway (Johnson, 1994, 1997, 2000; Merrit and Cooper, 2000). Negative feedback effects were observed following biological invasions of vegetation as a response to alterations of system dynamics (Mack and D'Antonio, 1998; Johnson et al., 2008). Bunn and Arthington (2002) consider that overall such regime alterations would also impact riverine fish and invertebrate communities, the strategies of which would be modified, acting to lower resilience of the system.

The idea that core properties like resilience and resistance can be manipulated in restoration measures is currently emerging (Smith et al., 2000; Lake et al., 2007). However, the specific sensitivity of HDRSs to natural and anthropogenic system alterations remains largely unknown. Many attempts at HDRS restoration or conservation attempt to predict future landform evolution from certain intrinsic or extrinsic emergent properties, and how far river managers can manipulate system controls (including landscape structure and biodiversity) to counterbalance the effects of major anthropogenic changes (Kollman et al., 1999; Edwards et al., 1999; Lake et al., 2007).

In the present context of major environmental changes, a practical question arises about our ability to develop sustainable, ecosystem-level management strategies using natural processes directly supported by the properties we describe in this paper (Rohde et al., 2005; Sambrook-Smith et al., 2006). We argue that the role of the interactions between biological and physical processes as controls of these core properties increasingly appears as crucial for system understanding and restoration (Bendix and Hupp, 2000; Tooth and Nanson, 2000; Gran and Paola, 2001; Corenblit et al., 2009). On the one hand, manipulating (restoring) river dynamics in order to improve resilience should buffer anthropogenic influence. On the other hand, one might expect a high sensitivity to manipulation, since such unstable systems offer a limited plant diversity that controls habitat dynamics and heterogeneity during and after disturbing events. Risks of functional and structural trajectory drifts remain limited as long as some keystone species (like pioneer Salicaceae in temperate HDRSs) or processes (dispersal, flow connection, sediment dynamics) are preserved. However, regional or global change may override local changes and no longer permit such species or processes to survive. More localized changes (e.g. invasions of introduced species) can initiate cascades of multiple changes (for invasions see Simberloff and Von Holle, 1999) affecting the fundamental properties of the system discussed in this paper. Such restoration or conservation measures suppose that physical-biological feedbacks and resistance-resilience trade-offs need to be identified and controlled.

Practical aspects of HDRS restoration by manipulating resilience and resistance would primarily depend on the restoration of the disturbance regime. Trying to mimic pristine hydrological conditions may not be the best solution in light of the myriad changes to the system. Furthermore, this would probably not be practicable in most cases. Preferably, one would first attempt to analyze the properties of hydrological regimes in natural HDRSs (periodicity, frequency, magnitude, extent) and their relationship to biological and geomorphic responses (biodiversity, ecological strategies, distributions). Then, the regulated regime could be modified to fit to an 'acceptable' model, taking into account the current species pool and sediment supply, in order to promote strategies that reflect the coexistence of resilience and resistance within the HDRS corridor. Here again, it would be unrealistic to try to restore communities or landforms by simply adding their components into the system. Preferably, management would initiate a new system trajectory, and progressively adapt the management practices (species control or introduction, topographic or hydraulic corrections) in order to preserve the system functionality.

Conclusion and perspectives

The review presented here highlights the importance and the complexity of biological and physical processes determining the resistance and the resilience of HDRSs. Such ecosystems mix resilience and resistance gradients, the location and the importance of which depends on both historical inheritance of landforms and vegetation, and on the colonization potential of labile fauna and flora. Our review suggests that resilience and resistance phenomena can locally coexist and that they promote the return of metastable states after major disturbances. We also argue that the biogeomorphic integrity of these systems depends, in part, on boundary effects that should be further examined in detail, both at the edges of the patches within the river corridor, and between the corridor and its surroundings.

The disturbance regime also contributes to the distribution in space of these fundamental system properties within the HDRS corridor. Hence, such systems potentially provide unique ecological and evolutionary mechanisms (Karrenberg et al., 2002; Tockner et al., 2003; Sadler et al., 2004). Fundamen-

tally, the study of resistance and resilience patterns within HDRSs constitutes a critical step in the understanding and prediction of the overall functioning of these systems. A crucial step for river scientists and managers is now to develop tools (i) to optimize the measurements of river system resilience and resistance; (ii) to identify key mechanisms controlled by them, and related functional pathways; and (iii), to manipulate them in order to stabilize the trajectory of HDRSs systems in a state that self-sustains a healthy functioning and continues to provide natural goods and services to society.

Acknowledgments

This paper was initiated during the European Science Foundation (ESF) Exploratory Workshop on "Linkages and feedbacks in highly dynamic, alpine, fluvial systems" in Cornino on the beautiful Tagliamento River, Italy, July 2008. The authors are grateful to the organizers of the workshop for their invitation. D. Corenblit acknowledges the post-doctoral research funding by the *Conseil Régional Auvergne*. the *Direction de l'Éducation, de l'Enseignement Supérieur et de la Recherche* and the *Fédération des Recherches en Environnement du site clermontois*. The research was also supported through the French research project "Waters & Territories. Water of the territory and territory of water: the restitution of fluvial dynamics and natural services provided to Society at stake" – "GALE&T" financed by the French Ministry of Ecology, Environment, Sustainable Development and Planning (MEEDDAT) and the French National Centre of Scientific Research (CNRS).

References

Allan, J. D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution and Systematics **35:** 257–284.

Amoros, C. and G. Bornette, 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology **47:** 761–776.

Andersson, E. C. Nilsson and M. E. Johansson, 2000. Effects of river fragmentation on plant dispersal and riparian flora. Regulated Rivers: Research & Management 1**6:** 83–89.

Arscott, D. B., K. Tockner, D. van der Nat and J.V. Ward, 2002. Aquatic habitat dynamics along a braided alpine river ecosystem (Tagliamento River, Northeast Italy). Ecosystems **5:** 802–814.

Barsoum, N., 2001. Relative contributions of sexual and asexual regeneration strategies in Populus nigra and Salix alba during the first years of establishment on a braided gravel bed river. Evolutionary Ecology **15:** 255–279.

Beechie, T. J., M. Liermann, M. M. Pollock, S. Baker and J. Davies, 2006. Channel pattern and river-floodplain dynamics in forested mountain river systems. Geomorphology **78:** 124–141.

Bellingham, P. J. and A. D. Sparrow, 2000. Resprouting as a life history strategy in woody plant communities. Oikos **89:** 409–416.

Bendix, J. and C. Hupp, 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes **14:** 2977–2990.

Bornette, G., E. Tabacchi, C. E. Hupp, S. Puijalon and J. C. Rostan, 2008. A model of plant strategies in fluvial hydrosystems. Freshwater Biology **53:** 1692-1705.

Brierley, G. J. and K. A. Fryirs, 2005. Geomorphology and River Management. Applications of the River Styles Framework. Blackwell Publishing, Oxford, 398 pp.

Brunsden, D., 2001. A critical assessment of the sensitivity concept in geomorphology. Catena **42:** 99–123.

Carpenter, S., B. Walker, J. M. Anderies and N. Abel, 2001. From metaphor to measurement: resilience of what to what? Ecosystems **4:** 765–781.

Chapin III, F.S., B.H. Walker, R.J. Hobbs, D.U. Hooper, G.H. Lawton, O. E. Sala and D. Tilman, 1997. Biotic control over the functioning of ecosystems. Science **277:** 500–504.

Chase, J. M. and M. A. Leibold, 2003. Ecological Niches: Linking Classical and Contemporary Approaches, Univ. of Chicago Press, Chicago, 221 pp.

Collier, K. J., S. Bury and M. Gibbs 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshwater Biology **47:** 1651–1659.

Connell, J.H., 1978. Diversity in tropical forests and coral reefs. Science **199:** 1302–1310.

Cooper, D. J., D. Andersen and R. A. Chimner, 2003. Multiple pathways for woody plant establishment on floodplains at local and regional scales. Journal of Ecology **91:** 182–196.

Corenblit, D., 2006. Structure et dynamique du paysage fluvial: étude des rétroactions entre processus hydro-géomorphologiques et dynamique de la végétation du Tech (Pyrénées orientales). Unpubl. Ph.D. Thesis, University Paul Sabatier, Toulouse III, France.

Corenblit, D., E. Tabacchi, J. Steiger and A. Gurnell. 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. Earth-Science Reviews **84:** 56–86.

Corenblit, D., A. M. Gurnell, J. Steiger and E. Tabacchi, 2008. Reciprocal adjustments between landforms and living organisms: Extended geomorphic evolutionary insights. Catena **73:** 261–273.

Corenblit, D., J. Steiger, A. Gurnell and R.J. Naiman. 2009. Plants intertwine fluvial landform dynamics with ecological succession and natural selection: a niche construction perspective for riparian systems. Global Ecology and Biogeography **18:** 507 – 520.

Coulthard, T. J., 2005. Effects of vegetation on braided stream pattern and dynamics. Water Resources Research **41:** W04003.

Crowl, T.A., C.R. Townsend, and A.R. McIntosh, 1992. The impact of introduced brown and rainbow trout on native fish: the case of Australasia. Reviews in Fish Biology and Fisheries, **2:** 217-241.

D'Antonio, C. and M. Thomsen, 2004. Ecological resistance in theory and practice. Weed Technology **18:** 1572–1577.

Davis, M. A., J. P. Grime and K. Thomson, 2000. Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology, **88:** 528-534.

Deharveng, L. and S. Lek, 1995. High diversity and community permeability: the riparian Collembola (Insecta) of a Pyrenean massif. Hydrobiologia **312:** 59–74.

Dole-Olivier, M. J., P Marmonier and J. L. Beffy, 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? Freshwater Biology **37:** 257–276.

Eder, E., W. Hödl, and R. Gottwald, 1997. Distribution and phenology of large Branchiopods in Austria. Hydrobiologia, **359:**13-22.

Edwards, P. J., J. Kollmann, A. M. Gurnell, G. E. Petts, K. Tockner and J. V. Ward, 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetlands Ecology and Management **7:** 141–153.

Edwards, R. T., 1998. The hyporheic zone. In: R. J. Naiman and R. E. Bilby (eds), River Ecology and management, Springer, New-York, pp. 344–365.

Elton, C. S., 1958. The ecology of invasions by animals and by plants, Methuen and Co., London, 181 pp.

England, L.E. and A.D. Rosemond, 2004. Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. Freshwater Biology **49:** 721-734.

Fisher, S. G., 1990. Recovery processes in lotic ecosystems: Limits of successional theory. Environmental Management **14:** 725–736.

Folke, C., S. Carpenter, B. Walker, M.Scheffer, T. Elmquvist, L. Gunderson and C. S. Holling., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution and Systematics **35:** 557–581.

Forman, R. T. T. and M. Gordon. 1986. Landscape Ecology, J. Wiley & Sons, New York, 619 pp.

Francis, R. A., D. Corenblit and P. J. Edwards. (In press.) Perspectives on biogeomorphology, ecosystem engineering and self-organisation in island-braided fluvial ecosystems. Aquatic Sciences (this volume).

Frissell, C. A, W. J. Liss, C. E. Warren and M. D. Hurley, 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management **12:** 199– 214

Gom, L. A. and S. B. Rood, 1999. Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. Canadian Journal of Botany **77:** 1095–1105.

Gran, K. and C. Paola, 2001. Riparian vegetation controls on braided stream dynamics, Water Resources Research **37:** 3275–3283.

Grime, J. P., 2001. Plant Strategies, Vegetation Processes and Ecosystem Properties, Wiley, Chichester, 250 pp.

Grubb, J. P. and A. J. M. Hopkins, 1986. Resilience at the level of the plant community. In: B. Dell, A. J. M. Hopkins and B. B. Lamont (eds.), Resilience in Mediterranean-Type Ecosystems, Dr. W. Junk Publishers, Dordrecht, Netherlands, pp. 21–38.

Gunderson, L. H. and C. S. Holling. (eds.), 2002. Panarchy: Understanding Transformations in Human and Natural Systems, Island Press, Washington DC., 507 pp.

Gunderson, L. H., 2000. Ecological resilience - in theory and application. Annual Reviews of Ecology and Systematics **31:** 425-439.

Gurnell, A. M. and G. E. Petts, 2006. Trees as riparian engineers: the Tagliamento River, Italy. Earth Surface Processes and Landforms **31:** 1558–1574.

Gurnell, A. M., G. E. Petts, D. M. Hannah, B. P. G. Smith, P. J. Edwards, J. Kollmann, J. V. Ward and K. Tockner, 2001. Riparian vegetation and island formation along the gravel-bed Fiume Talgliamento, Italy. Earth Surface Processes and Landforms **26:** 31–62.

Gyssels, G., J. Poesen, E. Bochet and Y. Li, 2005. Impact of plant roots on the resistance of soils to erosion by water: a review. Progress in Physical Geography **29:** 189–217.

Holling, C. S., 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4:** 1–23.

Holling, C. S., 1986. Resilience of ecosystems: local surprise and global change. In: W. C. Clark and R. E. Munn (eds.), Sustainable Development of the Biosphere, Cambridge University Press, Cambridge, pp. 292–317.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer and D. A. Wardled, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75:** 3–35.

Huston, M. A., 1994. Biological Diversity: the Coexistence of Species on Changing Landscapes, Cambridge University Press, Cambridge, 708 pp.

Johnson, P. T. J., J. D. Olden and M. J. V. Zanden, 2008. Dam invaders: Impoundments facilitate biological invasions into freshwaters. Frontiers in Ecology and the Environment **7:** 357–363.

Johnson, W. C., 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. Ecological Monographs **64**: 45–84.

Johnson, W. C., 1997. Equilibrium response of riparian vegetation to flow regulation in the Platte River, Nebraska. Regulated Rivers: Research and Management **13:** 403–415.

Johnson, W. C., 2000. Tree recruitment and survival in rivers: influence of hydrological processes. Hydrological Processes **14:** 3051–3074.

Jones, C. G., J. H. Lawton and M. Shachak, 1994. Organisms as ecosystem engineers. Oikos **69:** 373–386.

Jones, J., F. J. Swanson, B. C.Wemple and K. U. Snyder, 2000. Effects of roads on hydrology, geomorphology and disturbance patches in stream networks. Conservation Biology **14:** 76–85.

Junk, W. J., P. B. Bayley and R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences **106:** 110–127.

Kalliola, R. and M. Puhakka, 1988. River dynamics and vegetation mosaicism: a case study of the River Kamajohka, northernmost, Finland. Journal of Biogeography **15:** 703–719.

Karrenberg, S., Edwards, P.J. and J. Kollmann, 2002. The life history of Salicaceae living in the active zone of flood plains. Freshwater Biology **47:** 733-748.

Klimesova, J. and L. Klimes, 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. Perspectives in plant Ecology, Evolution and Systematics **8:** 115–129.

Kohler, S. L., D. Corti, M. C. Slamecka and D. W. Schneider, 1999. Prairie floodplain ponds: mechanisms affecting invertebrate community structure. In: D. P. Batzer, R. B. Rader and S. A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America: Ecology and Management, John Wiley and Sons, New York, pp. 711–730.

Kollmann, J., M. Vieli, P. J. Edwards, K. Tockner and J. V. Ward, 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. Applied Vegetation Science **2:** 25–36.

Lake, P.S., N. Bond and P. Reich. 2007. Linking ecological theory with stream restoration. Freshwater Biology **52:** 597-615.

Latterell, J., J. S. Bechtold, T. C. O'Keefe, R. Van Pelt and R. J. Naiman. 2006. Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic Mountains. Freshwater Biology **51:** 523–544.

Lavorel, S., 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. Diversity and Distributions **5:** 3–13.

Lepori, F. and N. Hjerdt. 2006. Disturbance and aquatic biodiversity: reconciling contrasting views. BioScience **56:** 809-818.

Lude, A., Reich, M. and H. Plachter. 1999. Life strategies of ants in unpredictable floodplain habitats of alpine rivers (Hymenoptera: Formicidae). Entomol.Gener 24: 74-91. Mack, M. C. and C. M. D'Antonio, 1998. Impacts of biological invasion on disturbance regimes. Trends in Ecology & Evolution **13:** 195–198.

Mack, M.C. and C.M. D'Antonio, 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution **13:** 195-198.

Macklin, M. G. and J. Lewin, 2008. Alluvial responses to the changing Earth system. Earth Surface Processes and Landforms **33:**1374–1395.

Mahoney, J. M. and S. B. Rood, 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands **18:** 634–645.

Malanson, G. P., 1993. Riparian Landscapes, Cambridge University Press, Cambridge, 296 pp.

Malard, F., K. Tockner, M. J. Dole-Olivier and J. V. Ward, 2002. A

landscape perspective of surface-subsurface hydrological exchanges in river corridors. Freshwater Biology **47:** 621–640.
Malard, F., U. Uehlinger, R. Zah and K. Tockner, 2006. Flood-pulse and riverscape dynamics in a braided glacial river. Ecology 87(3): 704–716.
May, R. M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature **269:** 471–477.
Merritt, D. M. and D. J. Cooper, 2000. Riparian vegetation and channel change in response to river regulation, a comparative study of regulated and unregulated streams in the green river basin, USA. Regulated Rivers: Research and Management **16:** 543–564.
Middleton, B., 2000. Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. Plant Ecology **146:** 169–184.
Miller, D. A. and P. Chesson, 2009. Coexistence in Disturbance-Prone Communities: How a resistance-Resilience Trade-Off Generates Coexistence via the Storage Effect. The American Naturalist, **173:** E32.
Mitchell, R. J., M. H. D. Auld, M. G. Le Duc and R.H. Marrs, 2000. Ecosystem stability and resilience: a review of their relevance for the conservation management of lowland heaths. Perspectives in Plant Ecology, Evolution and Systematics **3:** 142–160.
Mouw, E. B. J. and P. B. Alaback, 2003. Putting flood plain hyperdiversity in a regional context: an assessment of terrestrial- flood plain connectivity in a montane environment. Journal of Biogeography **30:** 87–103.
Muhar, S., Kainz, M., Kaufmann, M. and M. Schwarz, 1998. Erhebung und Bilanzierung flusstypspezifisch erhaltener Fliessgewässerabschnitte in Österreich. Österreichische Wasser- und Abfallwirtschaft **5/6:** 119-127.
Naiman R. J., J. J. Latterell, N. E. Pettit and J. D. Olden, 2008. Flow variability and the biophysical vitality of river systems. C.R. Geosciences **340:** 629–643.
Naiman, R. J. and H. Décamps, 1997. The ecology of interfaces, riparian zones. Annual Review of Ecology and Systematics **28:** 621–658.
Naiman, R. J., H. Décamps and J. McClain, 2005. Riparia: Ecology, Conservation and Management of Streamside Communities, Academic Press, 448 pp.
Naiman, R. J., S. R. Elliot J. M. Helfield and T. C. O'Keefe, 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. Hydrobiologia **410:** 79–86.
Newbold, J.D, J.W., Elwood, R.V., O'Neil, and W. Van Winkle, 1981. Measuring nutrient spiraling in streams. Canadian Journal of Fisheries and Aquatic Sciences, **38:** 860-863.
Nilsson, C. and K. Berggren, 2000. Alterations of riparian ecosystems caused by river regulation. BioScience **50:** 783–92
Odling-Smee, F. J.,, K. N. Laland and M. W. Feldman, 2003. Niche Construction: the Neglected Process in Evolution, Princeton University Press, Princeton, New York, 468 pp.
Paetzold, A., C. J. Schubert and K. Tockner, 2005. Aquatic Terrestrial linkages along a braided river: riparian arthropods feeding on aquatic insects. Ecosystems **8:** 748–759.
Peterson, G., C. R. Allen and C. S. Holling, 1998. Ecological resilience, biodiversity, and scale. Ecosystems **1:** 6–18.
Planty-Tabacchi, A. M., E. Tabacchi and M. J. Salinas Bonillo, 2001. Invasions of river corridors by exotic plant species : patterns and causes. In : G. Brundu et al. (eds), Plant Invasions, Backhuys Publ., Amsterdam, The Netherlands, pp. 221–234.
Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. DeFerrari and H. Décamps, 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology **10:** 598-607.
Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestergaard, B. D. Richter, R. E. Sparks and J. C. Stromberg, 1997. The natural flow regime. Bioscience **47:** 769–781.
Pollock, M. M., R .J. Naiman and T. A. Hanley, 1998. Plant species richness in riparian wetlands—A test of biodiversity theory. Ecology **79:** 94–105.
Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7:** 433–455.
Robinson, C. T., K. Tockner and J. V. Ward, 2002. The fauna of dynamic riverine landscapes. Freshwater Biology **47:** 661–677.
Rohde, S., M. Shutz, F. Kienast and P. Englmaier, 2005. River widening: an approach to restoring riparian habitats and plant species. River Research and Applications **21:** 1075–1094.
Roxburgh, S., K. Shea, and J. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology **85:** 359–371.
Sadler, J. P., Bell, D. and A. Fowles, 2004. The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. Biological Conservation **118:** 41-56.
Sambrook Smith, G. J., J. L. Best, C. S. Bristow and G. E. Petts, 2006. Braided Rivers, Process, Deposits, Ecology and Management, Special Publication of the International Association of Sedimentologists Series IAS, Blackwell Publishing, London, 396 pp.
Schumm, S. A., 1991. To Interpret the Earth: Ten Ways to Be Wrong, Cambridge University Press, Cambridge, U.K., 133 pp.
Simberloff, D. and B. Von Holle, 1999. Positive interactions of nonindigeneous species: the invasional meltdown. Biological Invasions **1:** 21–32.
Smith, G. J., J. L. Best, K. Tockner, F. Malard and J. V., Ward, 2000. An extension of the flood pulse concept. Hydrological Processes **14:** 2861–2883.
Southwood, T. R. E., 1988. Tactics, strategies and templets. Oikos **52:** 3-18.
Stachowicz, J. J., R. B. Whitlach and R. W. Osman, 1999. Species diversity and invasion resistance in marine ecosystems. Science **286:** 1577–79
Stanford, J., and J. Ward, 1992. Management of aquatic resources in large catchments: recognizing interactions between ecosystem connectivity and environmental disturbance. In: R. Naiman (ed.), Watershed management: balancing sustainability and environmental change, Springer, Berlin Heidelberg New York, pp 91–124
Steiger, J., E. Tabacchi, S. Dufour, D. Corenblit and J. L. Peiry, 2005. Hydrogeomorphic processes affecting riparian habitat within alluvial channel-floodplain river systems: a review for the temperate zone. River Research and Applications **21:** 719–737.
Tabacchi, E. and A. M. Planty-Tabacchi, 2001. Functional significance of species composition in riparian plant communities. Journal of the American Water Resources Association **37:** 1629–1637.
Tabacchi, E. and A. M. Planty-Tabacchi., 2005. Exotic and native plant community distributions within complex riparian landscapes: a positive correlation. Ecoscience **12:** 423–434.
Tabacchi, E., 1992. Colonization of periodically inundated interstitial habitats of an alluvial pond by invertebrates. Regulated Rivers: Research and Management **7:** 153–164.
Tabacchi, E., 1995. Structural variability and invasions of pioneer plant communities in riparian habitats of the middle Adour River (SW France). Canadian Journal of Botany **73:** 33–44.
Tabacchi, E., A. M. Planty-Tabacchi, L. Roques and E. Nadal, 2005. Seed inputs in riparian zones: implications for plant invasion. River Research and Applications **21:** 299–313.
Tabacchi, E., D. L. Correll, R. Hauer, G. Pinay, A. M. Planty-Tabacchi, and R.C. Wissmar, 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology **40:** 497–516.
Tal, M., K. Gran, A. Murray, C. Paola and D. Hicks, 2004. Riparian vegetation as a primary control on channel characteristics in multi-thread rivers. In: S.J. Bennett and A. Simon (eds.), Riparian Vegetation and Fluvial Geomorphology, Water Science and Applications Series 8, American Geophysical Union, Washington D.C, pp. 43–58.
Tetzlaff, D., C. Soulsby, P. J. Bacon, A. F. Youngson, C. Gibbins and I. A. Malcolm, 2007. Connectivity between landscapes and

riverscapes - a unifying theme in integrating hydrology and ecology in catchment science? Hydrological Processes **21:** 1385–1389.

Tockner, K., A. Paetzold, U. Karaus, C. Claret, and J. Zettel, 2006. Ecology of braided rivers. In: G. J. Sambrook Smith, J. L. Best, C.S. Bristow and G. E. Petts (eds.), Braided Rivers, Process, Deposits, Ecology and Management, Special Publication of the International Association of Sedimentologists Series, Blackwell Publishing, London: 339-359.

Tockner, K., C. Baumgartner, F. Schiemer and J. V. Ward, 2000. Biodiversity of a Danubian floodplain: structural, functional and compositional aspects. In: B. Gopal, W. J. Junk and J. A. Davis (eds.), Biodiversity in Wetlands: Assessment, Function and Conservation, Volume 1, Backhuys Publishers, Leiden, pp. 141–159.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer and J. V. Ward, 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshwater Biology **41:** 521–535.

Tockner, K., J. V. Ward, D. B. Arscott, P. J. Edwards, J. Kollmann, A. M. Gurnell, G. E. Petts and B. Maiolini, 2003. The Tagliamento River: A model ecosystem of European importance. Aquatic Sciences **65:** 239–253.

Tooth, S. and G. C. Nanson, 2000. The role of vegetation in the formation of anabranching channels in an ephemeral river, Northern plains, arid central Australia. Hydrological Processes **14:** 3099–3117.

Townsend, C., M. R. Scarsbrook and S. Doledec, 1997. The intermediate disturbance hypothesis, refugia and biodiversity in streams. Limnology and Oceanography **42:** 938–949.

van der Nat, D., A. P.Schmidt, K. Tockner, P. J. Edwards and J. V. Ward, 2002. Inundation dynamics in braided floodplains (Tagliamento River, northeast Italy). Ecosystems **5:** 636–647.

Walker, B. H., C. S. Holling, S. R. Carpenter and A. S. Kinzig, 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society **9:** 5.

Walker, B., 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology **9:** 747–752.

Ward, J. V. and K. Tockner, 2001. Biodiversity, towards a unifying theme for river ecology. Freshwater Biology **46:** 807–819.

Ward, J. V., K. Tockner, D. B. Arscott and C. Claret, 2002. Riverine landscape diversity. Freshwater Biology **47:** 517–539.

Ward, J. V., K. Tockner, U. Uehlinger and F. Malard, 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. Regulated Rivers: Research and Management **17:** 311–323.

Ward, J.V. and U. Uehlinger, 2003, (eds). Ecology of a glacial floodplain. Kluwer Academic Publishers, Dordrecht, NL.

Werritty, A., 1997. Short-term changes in channel stability. In : C. R. Thorne, R. D. Hey and M. D. Newson (eds.), Applied Fluvial Geomorphology for River Engineering and Management, J. Wiley & Sons, Ltd., Chichester, 47–65 pp.

Williams, P. A. and S. Wiser, 2004. Determinants of regional and local patterns in the floras of braided rivers in New Zealand. Journal of Biogeography **31(8):** 1355–1372.

Yashi, S. and M. Loreau, 1999. Biodiversity and ecosystem productivity in fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Science USA, **96:** 1463–1468.